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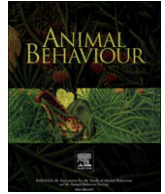
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Mate-guarding intensity increases with breeding synchrony in the colonial fairy martin, *Petrochelidon ariel*

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Extrapair paternity (EPP) is common in many socially monogamous species, influencing patterns of sexual selection and shaping many aspects of reproductive behaviour. However, factors explaining variation in the occurrence of EPP, both within and between populations, remain poorly understood. One ecological factor that has received considerable attention is breeding synchrony, but the proposed mechanisms remain contentious and the findings from the large number of correlational studies have been inconsistent. Mate guarding, a behavioural tactic to limit paternity loss, may be fundamental to any relationship between EPP and breeding synchrony. However, few studies have investigated how guarding behaviour varies with breeding synchrony, and the theoretical predictions are unclear. We examined how mate-guarding intensity in the colonial fairy martin varied with changes in breeding synchrony. To eliminate likely confounding effects of individual quality, we measured guarding intensity on multiple days during the fertile period of individual females and related this to daily variation in colony-level breeding synchrony. Similarly, we examined whether extrapair interest in fertile females varied with change in breeding synchrony. Both mate-guarding intensity and extrapair pursuit rate increased sharply several days prior to egg laying, before declining once laying commenced. When we controlled for this effect of female fertility status, guarding intensity increased with breeding synchrony. These novel findings suggest that the risk of paternity loss increases with breeding synchrony, at least among colonial species. Moreover, adjustment of guarding intensity to the risk of paternity loss may explain why most correlational studies do not reveal a relationship between EPP and breeding synchrony.

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In many socially monogamous species, females regularly copulate with males other than their social partner (Westneat et al. 1990; Birkhead & Møller 1992a; Griffith et al. 2002). The benefits to females of engaging in these extrapair copulations (EPC) remain poorly understood, but include such possibilities as insurance against the infertility of their social partner or improvement of the genetic quality of their offspring by mating with males that are

genetically superior or more compatible than their social mate (Jennions & Petrie 2000; Griffith et al. 2002). More obvious, however, are the potential costs of EPC to the female's social partner, because if they result in extrapair fertilization (EPF) he will sire fewer within-pair young and expend parental effort on unrelated offspring. Consequently, the males of many socially monogamous species show behaviours that appear to limit the likelihood of their partner engaging in EPC, reducing their risk of paternity loss (Birkhead & Møller 1998).

A commonly observed male tactic to reduce the likelihood of being cuckolded in birds is mate guarding, where males stay in close proximity to their partner during her fertile period (Beecher & Beecher 1979; Birkhead & Møller 1992a). Experimental studies show that mate guarding can be an effective way of minimizing paternity loss by both reducing the opportunities for females to seek EPC and limiting access to the female by other males (e.g. Chuang-Dobbs et al. 2001; Brylawski & Whittingham 2004; Komdeur et al. 2007). Moreover, by remaining in close proximity to their

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mate, males may maximize their own opportunity for within-pair copulations while she is fertile (Gowaty & Plissner 1987). However, guarding males are expected to incur some cost, and several studies show that mate guarding can be energetically costly (e.g. Møller 1987; Komdeur 2001; Low 2006) and may compromise their opportunity to gain additional social partners or EPC (e.g. Hasselquist & Bensch 1991; Marthinsen et al. 2005). Consequently, males are predicted to adjust their intensity of mate guarding in relation to their risk of losing within-pair paternity.

Perhaps the most significant factor determining a male's risk of within-pair paternity loss is the fertility status of his social mate. In birds, copulations that occur before the onset of laying can result in fertilizations because of sperm storage (which occurs for at least a week in passerines, Birkhead & Møller 1992b), although the chances of fertilization in the wild should generally increase closer to the start of laying because of passive sperm loss and last-male sperm precedence (Birkhead 1998). Females also remain fertile until the penultimate egg is laid (Birkhead & Møller 1992a; Birkhead et al. 1996), although strong declines in copulation rate are often observed after laying commences (Birkhead & Møller 1993). Consequently, males are predicted to guard their partner most intensely during this period of peak fertility and, consistent with this expectation, numerous studies have shown that mate guarding is most intense in the few days prior to the onset of egg laying (e.g. Birkhead 1982; Møller 1985; Riley et al. 1995; Krokene et al. 1996; Komdeur et al. 1999; Nicholls 2000; Low 2005).

The risk of cuckoldry may also vary with the synchrony of breeding across a population (Birkhead & Biggins 1987; Westneat et al. 1990). Typically, there will be some degree of asynchronous nesting in most avian populations, with early and later breeders generally more likely to experience lower synchrony than pairs breeding mid-season. The relationship between breeding synchrony and extrapair paternity (EPP) has received considerable attention, although empirical findings have been inconsistent. Some studies show an increase in EPP with synchrony (Stutchbury & Morton 1995; Stutchbury 1998), others show a decline (e.g. Conrad et al. 1998; Saino et al. 1999), but most reveal no systematic effect (Westneat & Sherman 1997; Bennett & Owens 2002; Griffith et al. 2002; Václav & Hoi 2002). In many species, mate-guarding behaviour and its effectiveness may be fundamental to the relationship between breeding synchrony and EPP (Birkhead & Biggins 1987; Westneat et al. 1990; Westneat & Gray 1998; Schwagmeyer & Ketterson 1999), and yet few studies have investigated whether guarding behaviour varies with changes in the level of synchrony within populations.

When synchrony is low, only a few females in the population will be concurrently fertile, and these individuals may attract more male-initiated EPC attempts than more synchronous females (Westneat et al. 1990), promoting the necessity for mate guarding (Wagner et al. 1996). Consequently, all else being equal, guarding may be expected to be most intense when the proportion of fertile females in the population is low (Wagner et al. 1996; van Dongen 2008). Alternatively, males may invest more effort into seeking EPC when a higher proportion of females in the population are fertile (greater synchrony) and/or synchrony may facilitate the ability of females to compare and choose among extrapair males, promoting their propensity to engage in EPC (Stutchbury & Morton 1995). In these two latter scenarios, the risk of cuckoldry may be predicted to increase with synchrony, resulting in more intense guarding to offset the greater risk.

These opposing predictions have been tested by comparing the intensity of mate guarding across pairs in relation to the current level of breeding synchrony, with two studies revealing a negative association between guarding intensity and local breeding synchrony, (black-throated blue warbler, *Dendroica caerulescens*:

Chuang-Dobbs et al. 2001; golden whistler, *Pachycephala pectoralis*: van Dongen 2008), and three others finding no effect (barn swallow, *Hirundo rustica*: Møller 1987; purple martin, *Progne subis*: Wagner et al. 1996; house sparrow, *Passer domesticus*: Václav & Hoi 2002). While these studies are illuminating, further data are clearly required, particularly in view of the inconsistent findings for the relationship between EPP and breeding synchrony. Furthermore, correlations may be confounded by differences in quality between individuals that influence the time at which they breed relative to others, the guarding ability of the male, and the likelihood of the female participating in EPC (Wagner et al. 1996). For example, males that breed relatively late, when synchrony is low, are likely to be younger or of lower quality and perhaps less capable of guarding their mate than birds whose partners lay earlier. One solution to this problem would be to manipulate the natural chronology of nesting in an attempt to decouple timing of laying and level of synchrony (e.g. Václav & Hoi 2002). Alternatively, variation in mate-guarding intensity can be examined within individual pairs in relation to daily changes in the synchrony of fertile females in the population, which would fully account for individual differences.

In this study, we investigated how female reproductive status and breeding synchrony influence within-pair mate-guarding behaviour in the socially monogamous fairy martin. Fairy martins breed colonially and both sexes invest extensively in all aspects of parental care (Magrath 1999). Nevertheless, extrapair paternity is very common, with a previous study finding that 20% of broods contained at least one extrapair offspring (Magrath & Elgar 1997). Mate-guarding behaviour has also been observed previously in the fairy martin (M.J.L. Magrath, personal observation). Moreover, extrapair males are known to attempt copulations with females gathering nesting material, and chase fertile females in aerial pursuits (Magrath 1999, unpublished data). Indeed, both guarding behaviour and extrapair chases and copulations appear to be common among the Hirundinidae in general (e.g. Beecher & Beecher 1979; Møller 1985; Lifjeld & Marstein 1994; Riley et al. 1995; Nicholls 2000).

In line with predicted fluctuations in the risk of within-pair paternity loss, we expected the intensity of mate guarding and also the frequency of extrapair chases to peak a few days prior to the onset of egg laying and extend into the laying period. More importantly, we aimed to examine how the intensity of mate guarding varies with breeding synchrony, allowing us to discriminate between opposing predictions and improve our understanding of how breeding synchrony relates to the frequency of extrapair paternity, both between and within populations.

METHODS

Study Population and General Field Methods

We studied fairy martins at three naturally occurring colonies under concrete bridges along the Colleambally outflow channel near Boorooban, New South Wales, Australia (34°56'S, 144°52'E), between September and November 2006. These three colonies (here designated A, B and C) were separated by at least 10 km and contained a maximum of 13, 45 and 53 concurrently active nests, respectively. Nests were considered active from the time nest-lining material appeared in the nest until the brood fledged (about 21 days after hatching) or the nesting attempt failed. The mean lay dates \pm SD (days) for colonies A, B and C were 13 November \pm 6.29, 18 October \pm 8.54 and 14 October \pm 8.91, respectively.

Fairy martins construct bottle-shaped mud nests, often at high densities. Once under construction, each nest was numbered and then checked every second day. Nest contents were inspected by

way of an artificial entrance, constructed prior to egg laying by drilling a hole through the side wall, plastering in a 10 mm section of plastic tubing (50 mm diameter), and filling the hole with a removable polystyrene plug. These inspections allowed us to estimate the date of first egg laying (assuming one egg laid per day), clutch size (maximum number of eggs in the nest), date of hatching (based on estimated age of oldest chick, see Magrath 1999), and nest success (at least one chick present after day 15) for all nests in the population. Clutch size varied between two and four eggs (mean \pm SD = 3.03 ± 0.51 eggs, $N = 105$) and we observed no evidence (appearance of two or more eggs in 1 day) of intraspecific brood parasitism. Nest inspections were conducted between 0900 and 1800 hours (local summer time) and colonies were visited for no longer than 60 min to minimize disturbance.

Most adults were caught in the nest when their brood was 7–12 days of age using a customized nest trap that permitted birds to enter but not leave the nest. Traps were checked every 15 min and installed for a maximum of 45 min to minimize disruption to feeding. Early in the season, some adults were also trapped using mist nets positioned parallel to the bridge. All adults were fitted with a numbered aluminium leg band for identification. Sex was determined by the presence (female) or absence (male) of a brood patch, because the sexes are otherwise monomorphic (Magrath 1999). Given that our interest in breeding synchrony was related to female fertility, we quantified synchrony on each day of the breeding season as the number of females in the colony that were fertile on that day, expressed as a proportion of all females in the colony (see Magrath & Elgar 1997). In line with estimates for other hirundinids (e.g. Beecher & Beecher 1979; Leffelaar & Robertson 1984; Nicholls 2000; Barber & Robertson 2007), we estimated the fertile period for female fairy martins to start from 5 days before egg laying up until the laying of the penultimate egg. The maximum level of synchrony in colonies A, B and C was 0.46, 0.53 and 0.36, respectively (i.e. proportion of females that were classified as fertile on the day of the season when this value was greatest).

The research was conducted with the approval of the Animal Experimentation Ethics Committee of the Australian National University.

Remote Monitoring System

At colony A, we used an electronic monitoring system to document the time and identity of birds entering nests. In this colony, all adults caught early in the season were fitted with a transponder (Trovan, Ltd., U.K.; 11×2 mm, 0.15 g) attached to the leg band. Transponders are small passive devices that emit a unique identification code when in the close proximity of a powered antenna. Existing nest entrances were replaced with an artificial entrance of similar dimensions and exterior appearance into which a customized antenna had been incorporated. Trovan readers (LID665) were used to decode the signal from the antennae and store the date, time (± 0.5 s) and unique transponder code of birds entering and leaving monitored nests. This method has previously been used in this population for collecting data on brood feeding rates (see details in Magrath et al. 2007). This monitoring system was used for assessing our assumptions about the identity and sequence of birds entering nests and not for collection of mate-guarding or extrapair pursuit data (see below).

Mate-guarding Intensity and ExtraPair Pursuit Rate

Typically, mate-guarding intensity is quantified as the proportion of time males spend in close proximity to their partner, or as the frequency of location changes initiated by the

female and followed by the male (Birkhead & Møller 1992a). These measurements are impossible to collect in fairy martins, because their spatial distribution is unpredictable and identification of individuals away from the colony very difficult. However, once the mud structure is complete females line their nest with grass and feathers before egg laying starts (Magrath 1999). During this period, pairs often arrive and enter their nest together, and we interpret this close following behaviour as mate guarding for three reasons. First, using the remote monitoring system (see above) and simultaneous video recording at two nests during the nest-lining stage, we found that birds entering the nests were always the male and female of the resident pair and that when both birds arrived in close succession, the following bird was almost always the male (18/19 occasions). Second, two birds entering the nest together often remained in the nest for an extended period (mean \pm SD = 77 ± 96 s, $N = 66$ observations at 11 nests) and typically departed together. Third, in several other hirundinids, males guard and closely follow their partner during her fertile period, with pairs often returning and departing from their nest together (Beecher & Beecher 1979; Lifjeld & Marstein 1994; Riley et al. 1995; Nicholls 2000).

The intensity of this guarding behaviour was quantified as the number of events when two birds entered the nest in close succession (less than 3 s apart) as a proportion of the total number of nest visits by one or more birds when no other bird was already inside the nest (i.e. the number of visits where two birds entered the nest in close succession expressed as a proportion of all visits). This measure is similar to that used in a study on sand martins, *Riparia riparia* (Nicholls 2000). On many occasions, we also observed that females with lining material were followed to the nest by one or more birds that did not enter the nest. In *R. riparia*, chasing birds were always male (Beecher & Beecher 1979) and we assumed that these chasing birds that did not enter the nest were male but not the female's social partner. We termed these events 'extrapair pursuits' and quantified their frequency as the proportion of all nest visit events where the lead bird (assumed to be female) was followed to within 1 m of the nest by one or more birds that did not enter the nest. On some occasions, guarding males may have followed their partner to the nest but did not enter. These events would have been assigned as extrapair pursuits, possibly leading to underestimation of guarding intensity and overestimation of extrapair pursuits. On other occasions, extrapair males may have followed unguarded females into their nests, and these events would have been incorrectly assigned as guarding. However, we have no reason to believe that these sources of error would have resulted in a systematic bias in relation to explanatory variables of interest (see below).

Nest visit data were recorded between 9 October and 25 November using video cameras positioned within the colony. Up to eight active nests could be observed from one camera and we used up to three cameras simultaneously. Video observations were conducted between 0800 and 1100 hours, because activity around the colony site was greatest in the morning (M. Hammers & M.T.L. Magrath, personal observation). Recording sessions lasted 1.5 h. In total, 337 sessions were recorded for 84 pairs of birds at the three colonies. The average number of observation sessions per pair \pm SE was 4.01 ± 0.36 (range 1–14). From each recording session a minimum of 15 continuous minutes of video were analysed for estimation of mate-guarding intensity and extrapair pursuit rate. If this 15 min period contained fewer than 10 visit events, subsampling of the session continued until 10 events had been recorded or until the conclusion of the entire 1.5 h session. On average, this equated to a mean \pm SE of 42.9 ± 1.4 (range 5–150) min of video and 9.4 ± 0.5 (range 1–57) nest visit events per observation session.

Statistical Analyses

To account for the hierarchical structure of our data, analyses were performed using the multilevel mixed-modelling procedure in MLwiN 2.02 (Rasbash et al. 2004). To examine variation in mate-guarding intensity, we constructed two-level models with pair identity (level 2), and each session of monitoring for that pair (level 1) as random parameters. This allowed the variation between all observation sessions of guarding intensity to be partitioned into either between-pair or within-pair. As guarding intensity was calculated as a proportion (proportion of visits that a pair arrived together), we used a binomial response model, with the total number of analysed visit events for each session used as the denominator of the proportion. The effect of female reproductive status on mate-guarding intensity was examined by entering the categorical variable 'Day relative to first egg', where the female's first egg equalled day zero. This variable was confined to the interval Day -9 (before which copulations are very unlikely to result in fertilizations, Birkhead & Møller 1992b) to Day 5 (2 days after the penultimate egg in the largest clutches of four). Colony identity was included to correct for possible differences in mate-guarding intensity between colonies. The timing of laying, relative to other pairs in the colony, was assessed by including laying date of the first egg relative to the median laying date (Relative laying date) for that colony (i.e. early breeders have negative values and late breeders positive values) as a continuous explanatory variable in the model. A similar model was constructed to examine variation in the rate of extrapair pursuits over the same interval.

Rather than absolute egg position in the clutch (1, 2, 3 or 4), guarding intensity may be related to the position of the egg relative to the last in the clutch, and therefore dependent on clutch size (which ranged from two to four). Using only observation sessions collected during laying ($N = 85$ sessions for 55 pairs), we explored this possibility by constructing a model with 'absolute egg position' and 'clutch size' as categorical variables along with their interaction term. A significant interaction would suggest that guarding intensity is (also) related to the relative position of the egg.

The effect of breeding synchrony on mate-guarding intensity was examined in another model that included only observation sessions collected during each female's fertile period (Day -5 to day of the penultimate egg). This analysis was further restricted to data from colony A where monitoring was very frequent and all pairs were observed on at least four occasions during each female's fertile period (mean \pm SD = 6.08 ± 1.00 occasions, $N = 12$ pairs) compared to an average of less than two at the other colonies (mean \pm SD = 1.93 ± 1.06 occasions, $N = 59$ pairs). For this model we first calculated the mean proportion of fertile females in the colony over the days on which the focal female was monitored during her fertile period (Mean PFF). We then calculated the deviation from this Mean PFF of the daily proportion of fertile females (Deviation from the mean PFF) for each day on which the focal female was observed. Entering both of these continuous variables into the model allowed us to assess whether within-pair mate-guarding intensity varied with daily changes in breeding synchrony (Deviation from mean PFF), but also to examine how between-pair variation in guarding intensity related to the mean level of synchrony experienced by each focal pair (Mean PFF). We controlled for variation attributable to female fertility status by including 'Day relative to first egg' as a categorical variable (see above). Relative laying date (see above) was also included in the model, most particularly to assess whether the relationship between guarding intensity and synchrony depended on the seasonal timing of laying. A similar model was constructed to examine variation in the rate of extrapair pursuits over the same period.

In all models the significance of potential explanatory variables was determined from the Wald statistic, which approximates the chi-square distribution, as each term was eliminated from the final model. Final models included a constant and all statistically significant ($P < 0.05$) explanatory variables. Interactions were tested but are only reported where statistically significant or of particular interest.

RESULTS

Mate Guarding, ExtraPair Pursuits and Female Reproductive Status

Mate-guarding intensity varied considerably over the 9 days before and 5 days after the first day of egg laying (Fig. 1a, Table 1). Generally, guarding intensity increased gradually from Day -9 to Day -5 before rising sharply and peaking on Days -3 and -2 when about 85% of nest visit events involved both members of the pair. This was followed by a steep decline to Day +1 (second egg) when guarding intensity fell to less than 10%, and stayed low over the remainder of the laying period. The overall level of mate guarding did not differ between colonies (Table 1), and was not related to relative laying date within the colony (Table 1).

The frequency of extrapair pursuits also varied markedly in relation to female reproductive status (Fig. 1b, Table 1), following a similar pattern to that observed for mate guarding. Generally, the extrapair pursuit rate increased to a peak on Days -3 and -2 before dropping to a low level after egg laying commenced. In contrast to guarding intensity, the overall frequency of extrapair pursuits differed between colonies (Table 1), and increased with relative laying date, although not quite significantly (Table 1).

In the subset of data restricted to observations during the laying period, guarding intensity declined strongly with absolute egg position ($P < 0.001$, $\chi^2_3 = 17.17$; Fig. 1a). This pattern did not differ between females with different clutch sizes (absolute egg position \times clutch size interaction; $\chi^2_6 = 1.28$, $P = 0.97$), indicating that guarding intensity appeared to be related to the absolute and not the relative egg position. However, most clutches contained three eggs (8×2 eggs; 50×3 eggs; 7×4 eggs), so the power of this analysis to reveal significantly different clutch size patterns was limited.

Mate Guarding, ExtraPair Pursuits and Breeding Synchrony

Over the period when females were estimated to be fertile (Day -5 to day of the penultimate egg), our within-pair analyses revealed that guarding intensity increased with an increase in the proportion of fertile females in the colony, our measure of breeding synchrony (Fig. 2, Table 2). Similarly, the frequency of extrapair pursuits also tended to increase with the proportion of fertile females in the colony (Fig. 2, Table 2). These correlations were not dependent on the relative laying date (Table 2).

In a comparison between pairs, mean mate-guarding intensity and mean extrapair pursuit rate during a female's fertile period were unrelated to the mean proportion of fertile females in the colony over the same period and not associated with the relative laying date (Table 2).

DISCUSSION

Mate-guarding Intensity and Female Reproductive Status

Mate-guarding behaviour is commonly observed among birds in the days before and sometimes during egg laying (e.g. Birkhead 1982; Møller 1985; Riley et al. 1995; Krokene et al. 1996; Komdeur et al. 1999; Low 2005). In this study, we observed a dramatic

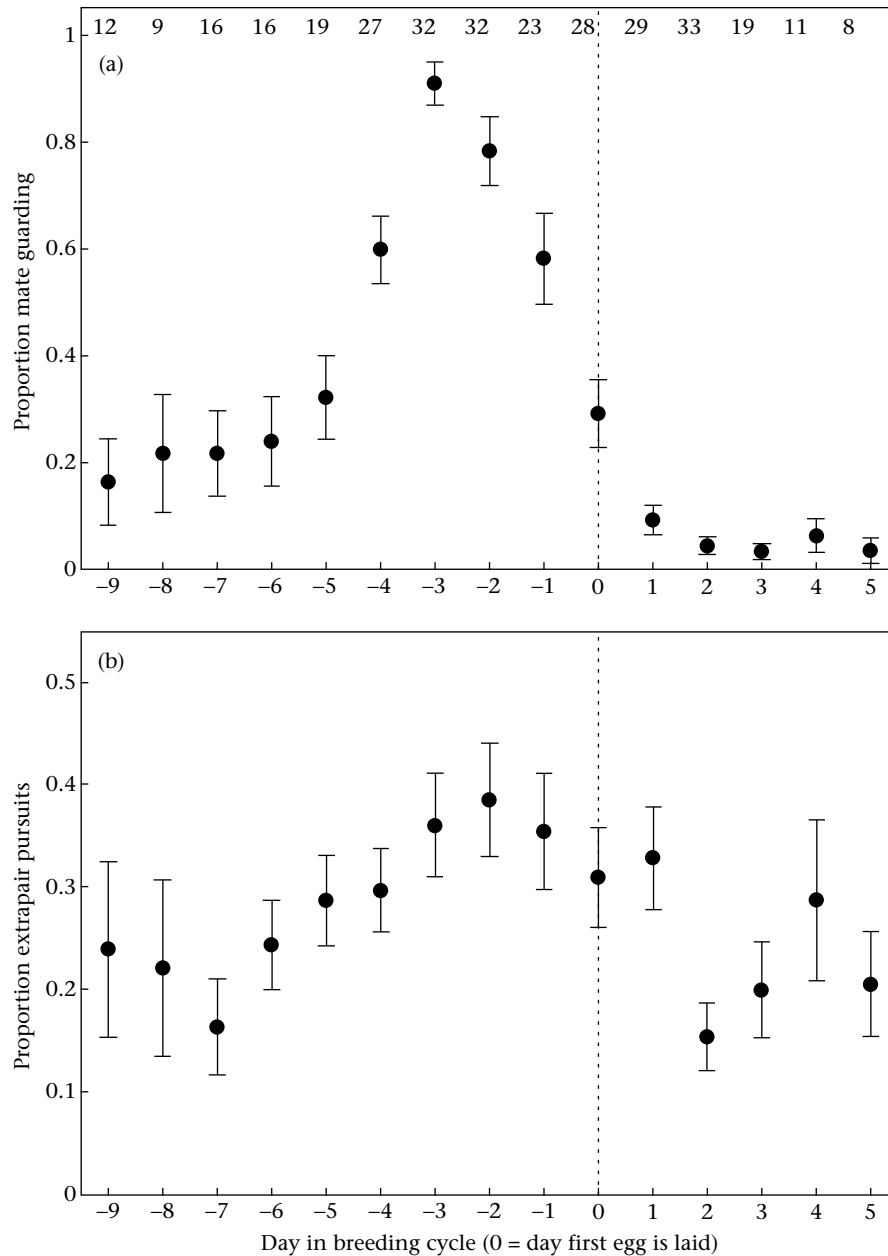


Figure 1. Relationship between female reproductive status and (a) mate-guarding rate and (b) extrapair pursuit rate. Female reproductive status is displayed as the number of days either side of the day of the first egg (Day 0). Means \pm SEs are shown for each day. Sample size of pairs for each day is shown at the top of (a). The dotted reference line shows the day on which the first egg in the clutch was produced. See Table 1 for model summaries of these data.

increase in the proportion of nest visits where the social pair entered together, several days prior to laying. This guarding behaviour increased abruptly from 5 days before the start of laying, peaking about 3 days before, and then declining to a low level on the first day of egg laying. The risk of within-pair paternity loss may also be expected to peak during the fertile period. Consistent with this expectation, females arriving at their nest during this period were more likely to be pursued by one or more birds that did not enter the nest. Moreover, the frequency of these extrapair pursuits followed a very similar profile to the mate-guarding intensity, also peaking 2–3 days before egg laying.

These strong temporal patterns of mate guarding and extrapair pursuits indicate that males must be using cues from the female that reveal her reproductive status. Males could use cues that the female reveals unavoidably, such as changes in flight ability caused by an

increase in body mass prior to egg laying (Beecher & Beecher 1979; Jones 1986; Low 2004) or collection of nesting material (Brown & Brown 1996; Magrath & Elgar 1997). Alternatively, the female may advertise her status actively to solicit guarding and/or interest from extrapair males. Possibly extrapair males, with less information about the female, may primarily use the guarding activity of the social male as an indicator of the female's fertility (Møller 1987; Westneat & Stewart 2003), which would account for the similarity in temporal pattern of guarding and extrapair pursuits.

In some birds, mate guarding continues until the clutch is almost complete (Birkhead & Møller 1992a), whereas in this study both guarding and extrapair pursuit rate declined to a low level after the first day of egg laying (Fig. 1a, b). One explanation for this decline is that most females were actually no longer fertile, during our observations of mate guarding, after the laying of their first egg.

Table 1

Model summaries examining the effect of female reproductive status on mate-guarding rate and extrapair pursuit rate

	df	χ^2	P	Estimate \pm SE
Mate-guarding rate				
Relative day to egg laying	14	234.17	<0.001	
Colony	2	0.79	0.675	
Relative lay date	1	0.054	0.816	0.005 \pm 0.021
Extrapair pursuit rate				
Relative day to egg laying	14	42.35	<0.001	
Colony	2	16.94	<0.001	
Relative lay date	1	3.23	0.072	0.020 \pm 0.011

Female reproductive status is defined in terms of days relative to laying of the first egg. The other potential explanatory variables tested in the models were colony and relative laying date. The models included 314 observation sessions at 84 nests from three colonies. Summaries were derived from binomial response, hierarchical, mixed models (see *Methods* for details).

Fairy martins generally lay before 0630 hours in the morning (personal observation), so fertilization of the next ovum is likely to have occurred before 0800 hours, especially in the wild situation when ova are probably fertilized by sperm already stored near the site of fertilization (Birkhead & Møller 1992a; Birkhead et al. 1996). Consequently, on the day that the penultimate egg was laid, females would no longer have been functionally fertile once our monitoring of guarding commenced after 0800 hours. Moreover, most clutches monitored during laying in this study comprised fewer than four eggs ($N = 58/65$ clutches), so in these cases elevated levels of guarding (at least by the time monitoring commenced) would not be expected beyond the day on which the first egg was laid. Consequently, in most cases the risk of paternity loss was probably negligible after the first day of egg laying. Alternatively, the general decline in guarding (apparent after Day–3; Fig. 1a), may have occurred because males were unable to sustain the energetic costs of guarding, even though the female remained fertile. However, this seems unlikely considering that extrapair pursuits also declined after the start of laying, unless guarding was the primary cue to incite extrapair pursuits.

The mate-guarding behaviour we observed is likely to limit access to the female by extrapair males, as guarding males were seen actively to chase away additional birds. Guarding may also represent a strategy by the social male to maximize his own opportunity for copulation (Gowaty & Plissner 1987; Birkhead & Møller 1992a). We occasionally observed females copulating with guarding males (presumably their social partner) at sites away from the colony when the female was collecting nesting material. However, pairs may also copulate within their nest, as they often remained there for an extended period during the female's fertile period. This is likely as pair copulations inside the nest have been reported for other hirundinids including the house martin, *Delichon urbicum* (Lifjeld & Marstein 1994; Riley et al. 1995) and cliff swallow, *Petrochelidon pyrrhonota* (Brown & Brown 1996).

Extrapair pursuits were never observed to result in copulation. However, at sites where birds aggregated to collect nest-lining material, individuals (presumably male) were often observed attempting to copulate with several other individuals (presumably females). Many of these attempts were resisted but some appeared to be successful. Most successful EPC may have occurred in a different context and at the initiation of the female, but these observations suggest that at least some male-initiated EPC attempts are successful.

Mate-guarding Intensity, Breeding Synchrony and ExtraPair Paternity

The mate-guarding intensity of male fairy martins increased with the proportion of fertile females in our intensively monitored

colony. This increase in guarding intensity was observed within pairs so was not confounded by date effects or possible differences in the quality of males or females that may influence their guarding behaviour. Instead, this increase suggests that the risk of paternity loss increases with population breeding synchrony. This may occur if some or all males in the colony increase their efforts to seek EPC or if females are more likely to solicit EPC when a higher proportion of females are simultaneously fertile.

Males may invest more in EPC effort when synchrony increases because the operational sex ratio becomes less male biased, improving the likelihood of an individual gaining an EPC, assuming that male-initiated EPC effort is related to EPF success. This scenario is supported by the finding that the rate of extrapair pursuits also tended to increase with synchrony, suggesting that at least some males in the colony increased their EPC effort. Similarly, in the closely related sand martin, both the intensity of extrapair chases and the frequency of copulation attempts with a model female increased with the proportion of fertile females, also suggesting that EPC effort is responsive to breeding synchrony (Nicholls 2000).

It remains unclear, however, whether a resident male's own reproductive status (i.e. nest building, mate guarding, incubating or nestling feeding) relates to his EPC effort. The proportion of guarding males in the colony will increase in direct relation to the proportion of fertile females, and guarding males may be highly motivated to seek copulations with both their social partner and extrapair females. However, mate guarding may constrain males from pursuing EPC, although this remains unclear. Shortly after the penultimate egg is laid, mate guarding is unnecessary but EPC effort may then be constrained by incubation, in terms of both time and physiological motivation (Magrath & Komdeur 2003). However, in a previous study on fairy martins, male contribution to incubation declined as the proportion of fertile females increased, suggesting that incubating males not only seek EPC, but also adjust EPC effort to mating opportunity (Magrath & Elgar 1997). Clearly, further information is required on when resident males are most likely to pursue and gain EPC, both in relation to their own reproductive status and the availability of fertile females in the population. One approach to this question may be to measure the testis size of individual males repeatedly during the breeding season. This should provide an indirect indication of the male's sexual activity over the course of his partner's reproductive cycle (Pitcher & Stutchbury 1998). Moreover, it is plausible that testis size may be adjusted to current levels of sperm competition, as testis mass across species is strongly correlated with the intensity of sperm competition (Birkhead & Møller 1992a).

Some EPC attempts are also likely to involve unpaired or nonresident males. Nonresident males gain extrapair fertilizations in tree swallows, *Tachycineta bicolor* (Kempnaers et al. 2001), and may even represent the majority of males attempting EPC in cliff swallows (Brown & Brown 1996). Nonresident male fairy martins may even aggregate at colonies when synchrony is highest to maximize their opportunity for EPC, exacerbating the risk of paternity loss for guarding males. The mean rate of extrapair pursuit varied between colonies, although our sample of colonies was insufficient to explore statistically whether this difference was related to any colony-level attributes. Nevertheless, it is noteworthy that the extrapair pursuit rate was highest in colony A which became established late in the season, was the most synchronous, and appeared to have the highest proportion of nonbreeding birds (unpublished data).

The increase in guarding intensity with synchrony could also result from a female preference for guarding males as extrapair mates. Stutchbury & Morton (1995) argued that when synchrony is high, females will have a greater choice of extrapair males that are in the same reproductive state as their social mate and therefore

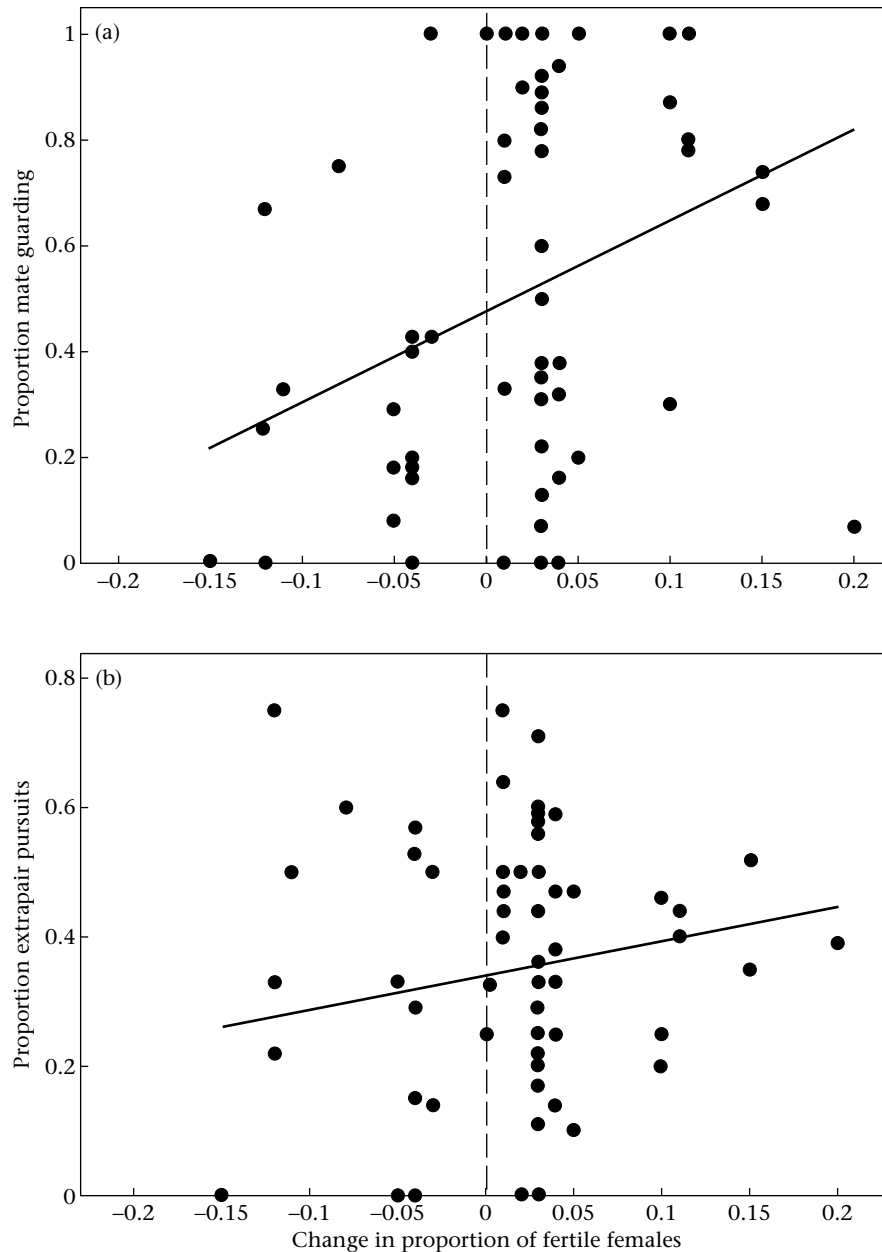


Figure 2. Relationship between breeding synchrony (estimated as the proportion of fertile females in the colony) and (a) mate-guarding rate and (b) extrapair pursuit rate within pairs of fairy martins. The solid lines show the model-predicted response in relation to daily change in the breeding synchrony. The points represent the values for individual observation sessions. The vertical reference line shows the line of zero deviation in daily proportion of fertile females from the mean proportion of fertile females on the days of observation. See Table 2 for model summaries of these data.

more easily compared. Consequently, the risk of paternity loss would increase with synchrony, resulting in males increasing their guarding intensity. This scenario assumes that successful EPC are primarily female initiated and function to enhance the genetic quality of their offspring. We have insufficient information to comment on these assumptions but clearly a more detailed understanding of the EPC behaviour of both males and females would help to reveal the mechanism underlying this relationship between mate guarding and synchrony (Westneat & Stewart 2003).

The observed increase in mate-guarding intensity with breeding synchrony is at odds with two previous studies that found males guarded less intensely when synchrony was high (Chuang-Dobbs et al. 2001; van Dongen 2008). One possible explanation for this difference is that these other studies were on territorial species

which would have regular interactions with far fewer conspecifics than the colonial fairy martins. This may fundamentally alter the extrapair mating strategies of both sexes in the context of breeding synchrony (Westneat & Sherman 1997; Westneat & Stewart 2003). Another possibility is that the relationship between guarding and synchrony that we observed was within rather than between individuals, avoiding the potentially confounding effects of individual quality differences. Highlighting the significance of this point, while we observed an increase in guarding intensity with synchrony within our focal pairs, there was no correlation between guarding intensity and synchrony when assessed across different pairs. This difference may occur if guarding intensity at the individual level is affected by factors such as quality or current food availability that set limits on or determine the necessity of mate

Table 2

Model summaries examining the effect of breeding synchrony on mate-guarding rate and extra-pair pursuit rate

	df	χ^2	P	Estimate \pm SE
Mate-guarding rate				
Relative day to egg laying	7	147.93	<0.001	
Relative lay date	1	2.99	0.08	0.06 \pm 0.03
Mean PFF	1	0.95	0.33	4.80 \pm 4.93
Deviation from mean PFF	1	16.48	<0.001	7.40 \pm 1.82
Extrapair pursuit rate				
Relative day to egg laying	7	12.15	0.10	
Relative lay date	1	1.46	0.23	0.04 \pm 0.04
Mean PFF	1	0.86	0.35	1.49 \pm 1.61
Deviation from mean PFF	1	2.82	0.09	2.35 \pm 1.40

The influence of breeding synchrony was partitioned into between-pair effects (Mean PFF) and within-pair effects (Deviation from mean PFF). Female reproductive status (defined as days relative to laying of the first egg) was included in the model because it strongly influences both mate-guarding and extrapair pursuit rates. The other potential explanatory variable tested in the model was relative laying date. The models included 73 observation sessions from 12 nests from a single colony that were observed on at least four occasions during the female's fertile period. Summaries were derived from binomial response, hierarchical, mixed models (see *Methods* for details).

guarding. The two previous studies in colonial species also found no across-pair relationship between guarding intensity and synchrony (Møller 1987; Wagner et al. 1996).

The apparent elevated risk of paternity loss that we observed with increasing synchrony could suggest that the frequency of extrapair paternity (EPP) increases with breeding synchrony. However, the observed increase in guarding intensity may be sufficient to compensate for the greater risk, resulting in the lack of any correlation between EPP and synchrony. Indeed, if high-quality males that are superior at mate guarding and/or are less likely to be cuckolded generally breed more synchronously, the level of EPP may even decline with synchrony. Consequently, even though the risk of paternity loss may vary with breeding synchrony, our finding that guarding is adjusted to the synchrony of fertile females may explain why most empirical studies report the absence of a correlation between synchrony and paternity. Manipulation of male capacity to mate guard (e.g. Chuang-Dobbs et al. 2001; Brylawski & Whittingham 2004) at periods of low and high breeding synchrony or the colony-level manipulation of breeding synchrony (e.g. Václav & Hoi 2002) could be useful approaches to further our understanding of the relationships between mate guarding, breeding synchrony and extrapair paternity.

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